Hydroacoustical evidence of the expansion of pelagic swarms of *Munida gregaria* (Decapoda, Munididae) in the Beagle Channel and the Argentine Patagonian Shelf, and its relationship with habitat features

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ABSTRACT

Squat lobsters are highly diversified and widespread decapods, of which only three species form pelagic swarms. Here we infer the expansion of *Munida gregaria* populations in the Beagle Channel and the Argentine Patagonian Shelf by means of acoustic surveys of pelagic swarms. We also describe the habitat characteristics in which these swarms occur. Acoustic data was collected during three multidisciplinary scientific cruises on board of the *R/V Puerto Deseado* during 2009, 2012 and 2014. Despite differences in the environmental conditions between the two surveyed areas, between 2009 and 2014 pelagic swarms increased their occurrence and abundance both in the Beagle Channel and on the Argentine Patagonian Shelf. Towards the end of the studied period, pelagic swarms of *M. gregaria* occurred in new locations, supporting the notion of a population expansion. Within the Beagle Channel swarm expansions were more marked than on the Patagonian Shelf. We here postulate that *M. gregaria* expansions occur in association with productive areas of the Argentine continental shelf, such as frontal zones, favoured by the squat lobster phenotypic plasticity that permit to exploit resources in both the neritic and benthic environments. At a regional scale on the Patagonian Shelf, three main groups of pelagic swarms of *M. gregaria* were clearly associated to respective frontal zones. The information presented here is necessary to understand fluctuations in both distribution and abundance patterns of a key species on the Argentine continental shelf. These fluctuations could be direct or indirect indicators of changes in the ecosystem.

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1. Introduction

The dynamics of population expansions have been subject of study for a long time. Decapods, like other marine taxa, have a potentially extensive larval dispersal and specific habitat preferences. Movement patterns of juveniles and adults are generally rather restricted, although extensive migrations have been reported for some species. In addition, early life history traits, such as reproductive parameters (e.g. fecundity, egg size and brood period) affect recruitment in marine decapods (Cobb et al., 1997) and, in consequence, are relevant in population dynamics in combination with extrinsic environmental factors (e.g. temperature, salinity, and food) and intra- (e.g. agonistic interactions) and interspecific relationships (predator-prey cycles). Furthermore, in this context, animal populations are spatial objects because their structure and functioning depend on a spatial perspective (Roa and Tapia, 2000). In particular, populations of decapod crustaceans like lobsters, crabs and shrimps exhibit defined spatial structures linked with habitat features and requirements (Fogarty and Botsford, 2006). These spatial structures

as a result of interaction with the environment seem to be particularly more important in decapod species that form swarms and shoals. This type of behaviour makes these species spending much of its life in the water column, a more heterogeneous environment (temperature, circulation and food resources) than the sea-bottom.

Squat lobsters are highly diversified and widespread decapods (Ahyong et al., 2010; Baba et al., 2008; Schnabel et al., 2011). From the six known families, Munididae is the largest with 387 species (Macpherson and Baba, 2011) of which only a few species have a pelagic phase and swarming behaviour during their life span: *Pleuroncodes planipes*, *Pleuroncodes monodon* and *Munida gregaria*. These species form pelagic swarms from the surface to the bottom of the water column and due to the physical properties of their bodies, they are easily detectable by echosounding (Diez et al., 2012; Gomez-Gutierrez et al., 2000; Gutiérrez et al., 2008; Robinson and Goómez-Gutiérrez, 1998). *M. gregaria* occurs around New Zealand and Australia, and around southern South America (SSA), from 41°S to 55°S in the Pacific Ocean and from 35°S to 55°S in the Atlantic Ocean (Baba et al., 2008; Schnabel et al., 2011; Spivak, 1997). In SSA *M. gregaria* is an ecologically important species due to its role in trophic webs representing the direct link between producers/particulate organic matter and top predators (Lovrich and Thiel, 2011; Romero et al., 2004). *M. gregaria* shortens

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the trophic web, making more efficient the energy transfer to higher levels (Kashkina and Kashkin, 1993). *M. gregaria* has two morphs: "gregaria" and "subrugosa" (Diez et al., in press), formerly considered two species: *M. gregaria* (Fabricius, 1793) and *Munida subrugosa* (Dana, 1852) though recently distinguished as one and synonymized (Baba et al., 2008; Pérez-Barros et al., 2011, 2010, 2008). The "gregaria" morph is the postmetamorphic pelagic phase that after a variable period of time eventually settles on the sea bottom and can perform vertical migrations. "Gregaria" can settle immediately after the metamorphosis to the first juvenile stage or swarms up to six months (Varisco and Vinuesa, 2010; Zeldis, 1985). Findings of swarms with individuals of age 1 to 2 years suggest that they can remain in the water column even longer (Diez et al., 2012; Madirolas et al., 2013). The "subrugosa" morph is exclusively benthic and adults of the two morphs can coexist in the benthic community (Diez et al., 2012; Tapella, 2002). Both morphs are easily distinguished by different morphological features (Tapella and Lovrich, 2006), with "gregaria" having adaptations which make it thrive in the water column (Tapella and Lovrich, 2006; Zeldis and Jillett, 1982).

Occurrence of swarming behaviour in Southern South America has been irregular or not properly detected. So far, only a single record of swarming *M. gregaria* is available from the SE Pacific coast (Tabeta and Kanamaru, 1970) and records of swarming in SSA are fragmentary (Kawamura, 1976; Matthews, 1932; Rayner, 1935), indicating that the shoaling periods do not seem to be as regular as those reported off New Zealand (Zeldis and Jillett, 1982). There, the occurrence of swarms is clearly seasonal occurring right after larval metamorphosis (Zeldis, 1985). However, the swarming period may extend in the season depending on environmental features (Zeldis, 1985). *M. gregaria* swarms had not been detected neither in the Beagle Channel in 1998–2001 by direct observation (Tapella, 2002), nor during regular acoustic surveys for fish assessment carried out off the Patagonian Shelf in 1990–2005 (Madirolas et al., 2013). However, since 2008 the occurrence of these aggregations in the Beagle Channel (Diez et al., 2012) have coincided with those recorded in other locations of SSA, particularly off the Patagonian coast e.g. Golfo San Jorge (Fig. 1) (Madirolas et al., 2013; Varisco and Vinuesa, 2010). These events also correspond with a change in the proportion of both morphs at the sea-bottom. In the Beagle Channel and between 1993 and 2003, *M. gregaria* "subrugosa" was the dominant morph, comprising at least 50% of the biomass of the benthic community and at least 85% of both morphs (Arntz and Gorny, 1996; Pérez-Barros et al., 2004). More recently, the proportion of benthic morphs inverted to 95% of the "gregaria" morph. In other locations where pelagic swarms of *M. gregaria* occur, changes in the proportions of benthic morphs were also evident. In the Golfo San Jorge the "subrugosa" morph was the most abundant until 2005; however, in 2011, proportions of both morphs showed significant changes with a 66% of occurrence of "gregaria" (Ravalli et al., 2012; Fig. 1).

The Patagonian Shelf covers approximately 12° in latitude and 200 km width, with a gently slope and several areas of high primary productivity (Rivas et al., 2006). Waters over the continental shelf are sub-Antarctic. The general circulation in this area is towards northeast and influenced by large tidal amplitudes, substantial freshwaters discharges, and high wind speeds (Matano et al., 2010). To the south, there is a direct inflow of cold Antarctic waters from branches of the Antarctic Circumpolar Current, incoming through the Le Maire Strait. To the east and over the continental shelf break, the Malvinas Current is a narrow and deep northward jet (Matano et al., 2010; Sabatini et al., 2004). In the inner-shelf, south of ca. 49°S, there is a well-defined jet, known as the Patagonian Current, that is generated through the interaction of tidal currents and the diluted waters discharged through the Magellan Straits (Palma et al., 2008). The extension of the Patagonian continental shelf allows for the development of at least four different mesoscale fronts, which are areas with high biological production (Acha et al., 2004).

In the present study we use acoustic surveys to estimate the expansion of pelagic swarms of *M. gregaria* in the Beagle Channel and the Argentine Patagonian Shelf between 2009 and 2014. We also describe the habitat characteristics in which these swarms occur. The information presented here is necessary to understand fluctuations in both distribution and abundance patterns of a key species on the Argentine continental shelf.

2. Methods

2.1. Study area

Acoustic data was collected during three multidisciplinary scientific cruises on board of the *R/V Puerto Deseado* during December 2009 (16 days), April 2012 (20 days) and April 2014 (7 days) (Fig. 1). The first survey was conducted along the Patagonian Shelf and continental slope from the Península Valdés to Ushuaia, including the Beagle Channel, Burdwood Bank and waters around Isla de los Estados/Staten Island (Fig. 1). The second survey was from Ushuaia to Mar del Plata (57° 33′ W 38° S) along the mid shelf. The third survey was carried out in the Beagle Channel and Atlantic coast off Tierra del Fuego (Fig. 1). Data acquisition was performed continuously onboard during both day and night. Satellite images on sea surface temperature, Chl-*a* concentration and particulate organic carbon concentration were used to estimate habitat features.

2.2. Acoustic data recording and post-processing and concurrent net sampling

Acoustic data was recorded with a SIMRAD EA400 single beam echosounder at 12 kHz and 200 kHz (Table 1). Calibration of the echosounder was performed prior to each survey following the standard routines (Foote et al., 1987). The calibration target consisted of a WG38 solid metal sphere used as a standard for signal amplitude calibration at the given sound frequencies (Foote and MacLennan, 1984; Kloser et al., 2002). The digital acoustic records were stored in data files in a computer for their future further post-processing. Data processing consisted of the echointegration of the acoustic signal (MacLennan and Simmonds, 1992) using the Echoview v4.10 post-processing software (Myriax Pty, Australia). Echograms of 20 log R time-varied gain obtained only at 200 kHz were processed to isolate the concentrations of *M. gregaria* and to further describe their spatial and energetic characteristics. The averaging distance for echointegration (E.S.D.U.) was 1 nm (MacLennan and Simmonds, 1992). Swarms of *M. gregaria* were not detected at 12 kHz, not even by using the lowest possible minimum threshold level (−85 dB). A minimum threshold of −75 dB was applied to the 200 kHz signal in order to remove unwanted contributions from noise. Additionally, swarm metrics were measured by means of the Echoview's School detection module.

Pelagic aggregations of *M. gregaria* were identified in different ways. (i) By visual assessment of the echograms according to previous knowledge of the swarm morphology (Diez et al., 2012; Madirolas et al., 2013). Morphometric parameters of swarms as S_v mean (dB), length (m), height (m), cross-sectional perimeter (m), and cross-sectional area were included in this visual assessment and analysis (Diez et al., 2012). (ii) With vertical nektonic trawls. Samples were taken with a net of 1 m of mouth diameter and 10 mm of mesh size. Ad hoc sampling stations were established according to the presence of swarms in the echograms. If sea conditions were adequate and when a swarm was detected in the echogram the vessel stopped and the net was lowered to the depth where the swarm was located. (iii) Incidental catches of *M. gregaria* present in other planktonic nets during surveys were also used to validate the acoustic records. Furthermore, benthic samples of *M. gregaria* were taken with a bottom trawl net of 1.8 m mouth width and 10 mm mesh size. All caught animals were preserved in 5% formalin seawater. In the laboratory, individuals were sexed and their size was
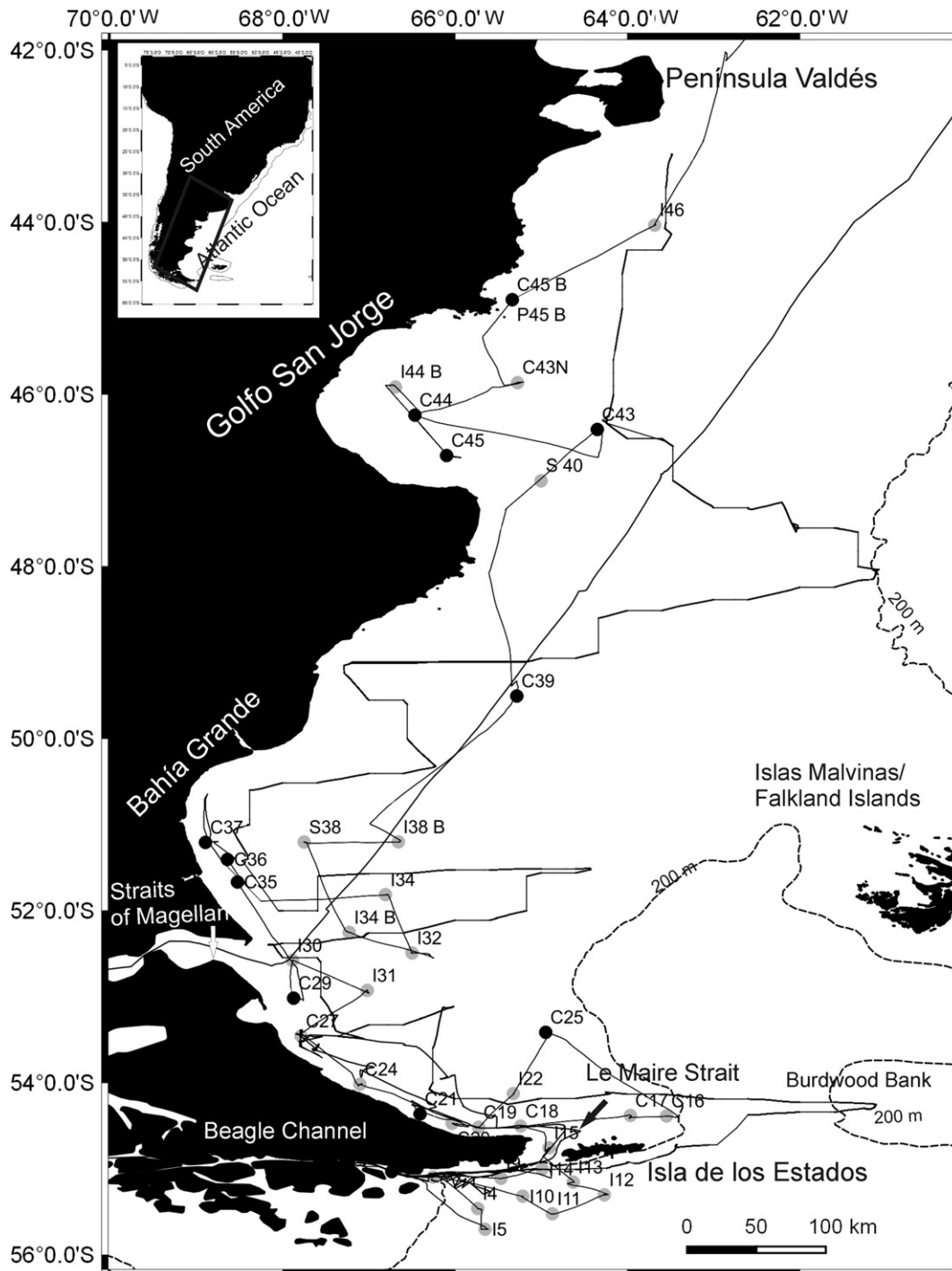
Fig. 1. Track line of R/V Puerto Deseado during acoustic surveys in 2009, 2012 and 2014. Circles and numbers denote fishing stations. Black circles are stations with *Munida gregaria* captures, grey circles show stations without *M. gregaria* captures.

estimated by measuring their carapace length (CL) with an electronic caliper to the nearest 0.01 mm.

2.3. Environmental data and statistical analysis

Monthly averages of ocean colour (Chl-*a*), sea surface temperature (SST) and particulate organic carbon (POC) on the Argentine Patagonian Shelf for December 2009, April 2012 and April 2014 were obtained from Aqua-MODIS satellite images in HDF format (http://oceancolor.gsfc. nasa.gov), at 4-km spatial resolution. SAGA, GRASS and GDAL

complements of QGIS Chugiak 2.4.0 were used for image handling and to calculate monthly averages of Chl-*a* (mg·m^{-3}), SST (°C) and POC (mg·m^{-3}). Bathymetric data was derived from GEBCO at a spatial resolution of 30 arc-second intervals (0.0083° or ca. 1 km). Satellite images from the Beagle Channel with an adequate resolution are lacking, and therefore analyses on habitat characteristics were only performed for the Patagonian Shelf.

In order to calculate the values of the habitat parameters for each acoustic record of swarms of *M. gregaria* on the Patagonian Shelf, all data was incorporated into a geographic information system (GIS)

Table 1
Echosounder parameters during acoustic surveys in the Beagle Channel and Argentine continental shelf and post-processing software working parameters.

Frequency (kHz)	200
Beam type	Single
Pulse length (ms)	1.024
Maximum power (W)	1000 W
Absorption (dB/km)	0.04566 dB/m (2009)
	0.0484 dB/m (2012–14)
Transducer gain	24.8 dB
Sound velocity (m/s)	1500 m/s
Post-processing software	Echoview 4.10
S_v threshold (dB)	−75

using QGIS 2.4.0-Chugiak (www2.qgis.org.ar) and projected into a Lambert Azimuthal Equal-area (South Pole) projection. To identify patterns in the data, a principal component analysis (PCA) on the four environmental variables was estimated for each swarm. From the PCA, the coefficients on each axis were transferred to a non-hierarchic analysis (K-means algorithm, Euclidean distance) with the aim to characterize the separated groups. For each zone, one-way ANOVAs were performed to evaluate inter-annual differences in the volume backscattering coefficient (S_v) and the nautical area scattering coefficient (NASC). Tukey tests were carried out a posteriori when differences in the ANOVA were significant. Both multivariate and univariate analyses were performed with the Infostat v.2015 statistical package (Di Rienzo et al., 2011).

3. Results

The three surveys visited the Beagle Channel and the Patagonian Shelf (Fig. 1, Table 2). A total of 2057 acoustic records assigned to *M. gregaria* were registered in these surveys, ranging from very small patches to very large swarms.

3.1. Horizontal and vertical distribution of swarms

3.1.1. Beagle Channel
The position of the swarms in the water column and their vertical structure were variable. In some cases, squat lobsters formed relatively compact and dense swarms, in other cases a layer of squat lobsters extended for tens of kilometers. In occasions, swarms were composed by more than one layer of individuals in the water column.

In the Beagle Channel, pelagic swarms showed an expansion from 2009 to 2014. The horizontal distribution showed an increment in the percentage of occupation of the surveyed area (Table 2). In this area,

Table 2
Basic parameters describing acoustic data of pelagic swarms of *Munida gregaria* found during acoustic surveys in the Beagle Channel and Patagonian Shelf.

		Year		
		2009	2012	2014
	Total track (km)	3054	4924	1252
Beagle Channel	Swarms S_v mean (dB)	−59.07	−61.63	−61.36
	Swarms S_v max (dB)	−47.8	−41.17	−46.46
	Survey NASC mean (m²/nm²)	1557.75	785.96	453.94
	Survey NASC max (m²/nm²)	11,567.97	18,193.87	9303.77
	Swarm mean depth (m)	20.52	27.83	19.02
	Occupancy of survey area %	19.21	34.00	71.74
Patagonian Shelf	Swarms S_v mean (dB)	−68.49	−60.79	−61.97
	Swarms S_v max (dB)	−50.59	−39.69	−50.90
	Survey NASC mean (m²/nm²)	129.00	782.11	424.92
	Survey NASC max (m²/nm²)	6494.38	30,303.95	3416.39
	Swarm depth (m)	73.11	24.03	22.33
	Occupancy of survey area %	7.15	11.05	13.49

the percentage of occupation in 2014 tripled that of 2009. At the beginning of the study few big swarms (ca. 8000 m length, ca. 40 m height) were recorded mainly in the eastern Beagle Channel (Fig. 2). By contrast, in 2014 numerous smaller swarms of *M. gregaria* were observed throughout the area (maximum 2100 m length, 20 m height) (Fig. 2). The extent of the geographical distribution of the nautical area scattering coefficient (NASC) assigned to *M. gregaria*, was higher in 2009 but showed similar values in 2012 and 2014 (One-way ANOVA, F = 4.17, p < 0.05; Tukey test p < 0.05) (Table 2; Fig. 2). However, the mean value of the volume backscattering coefficient (S_v) showed no variations among years (One-way ANOVA, F = 2.01, p > 0.05), indicating that swarms had similar average acoustic energy during the study period (Table 2). The vertical distribution in this area showed that the mean depth of swarms of *M. gregaria* was <30 m during the study period (Table 2).

3.1.2. Argentine Patagonian Shelf
The coverage of the studied area was different among the three surveys. While the coverage of the Beagle Channel area was quite similar, the acoustic sampling of the Patagonian Shelf was different in each survey and particularly less intense in 2014. Although the 2012 survey results suggest a clear increment of the abundance of squat lobsters and also of area occupied by swarms compared to 2009, the 2014 survey also indicates that, despite the lower prospected area, the change was still evident (Table 2). The horizontal distribution of pelagic swarms of *M. gregaria* in 2009 showed shoals mainly in the southeastern part of the Atlantic coast of Tierra del Fuego and on the shelf break (Fig. 3). In 2012, swarms were dispersed over the mid-shelf and along the south coast of the continent, with shoals of high acoustic intensity in the inner shelf, along the Bahía Grande and Golfo San Jorge (Fig. 3). At the end of the study (2014), even if the survey sampling intensity over the Patagonian platform was lower compared to the previous surveys, pelagic swarms were observed only off the southeastern coast of Tierra del Fuego, where shoals with high acoustic intensity were located mainly in the Le Maire Strait (Fig. 3). The horizontal distribution of NASC assigned to *M. gregaria* was different between years (One-way ANOVA, F = 133.03, p < 0.0001; Tukey test p < 0.05) with an increase by 4.5 times in 2012 compared to 2009 and a subsequent decrease in 2014 to a half of the 2009 values (Table 2; Fig. 3). On the Patagonian Shelf the S_v showed a similar pattern to NASC, with a pronounced increment in 2012 (One-way ANOVA, F = 508.4, p < 0.0001, Tukey test p < 0.05; Table 2).

The mean depth of the swarms observed in this area was similar to that of the Beagle Channel (<30 m), except for the 2009 survey when the mean depth of swarms was found deeper in the water column (Table 2). A decreasing trend in the average S_v with the depth of the swarms was observed, especially in the Patagonian Shelf area (Fig. 4).

3.2. Composition of pelagic swarms and benthic aggregations

Size frequency distributions of swarms and benthic aggregations were approximately unimodal (Figs. 5 and 6). However, different swarms were composed of different sizes. In some swarms only sexually undetermined individuals were found (mode = 10.31 mm CL, Fig. 5), whereas in other swarms bigger individuals were observed (mode = 21.07 mm CL, Fig. 5). During the study period, no pelagic swarms were found between the eastern entrance of the Straits of Magellan and the northern tip of the Le Maire Strait, Tierra del Fuego (Fig. 3). In this area, benthic samples showed aggregations composed of high proportions of only the subrugosa morph of *M. gregaria* (Fig. 6).

3.3. Habitat features

The PCA showed that the two first components explained over ca. 80% of the variability in the data set of distribution of pelagic swarms of *M. gregaria* on the Patagonian Shelf. Swarms with a high PC1 value
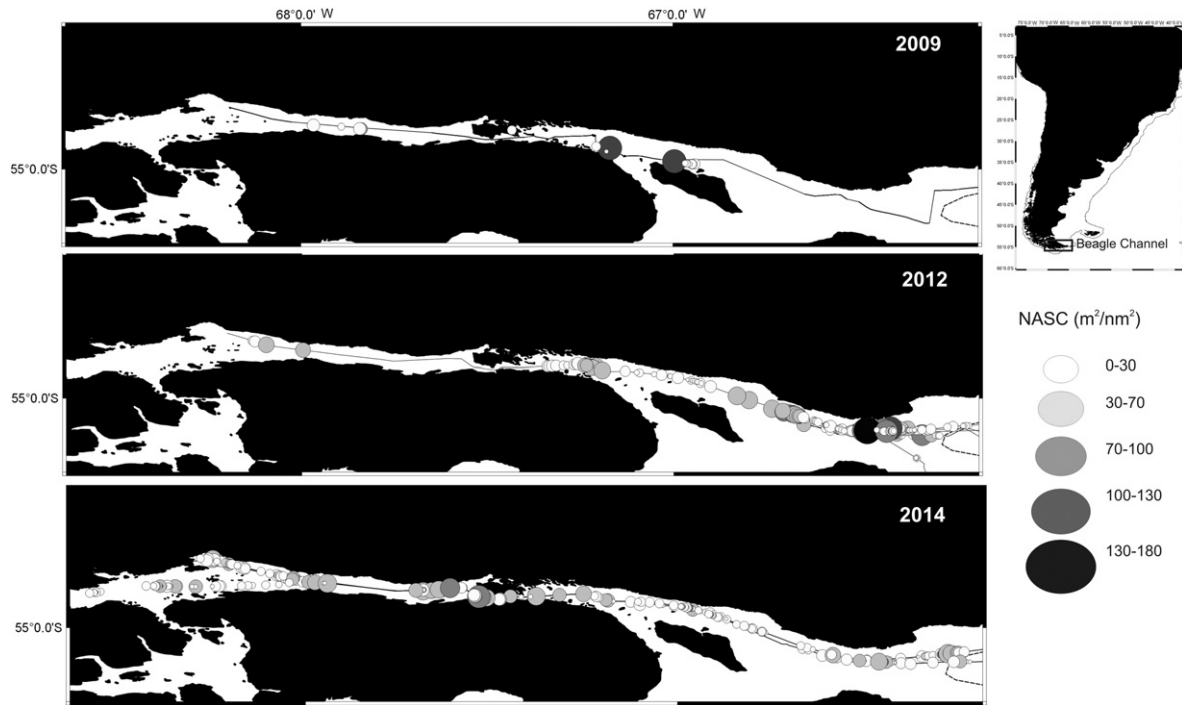
Fig. 2. Horizontal distribution of pelagic swarms of *Munida gregaria* in three years in the Beagle Channel. The size of circles is proportional to the NASC (m²/nm²).

occurred in waters with high [Chl-*a*] and POC, while swarms with a high PC2 value occurred mainly in the deepest surveyed waters of the outer shelf (Table 3). When the coefficients of each environmental variable of each PC were transferred to a non-hierarchic cluster analysis (*K* means), three groups were differentiated in relation to the environmental conditions where swarms of *M. gregaria* occurred (Fig. 7). Group 1 included swarms of *M. gregaria* from the southeastern part of Tierra del Fuego, through the Le Maire Strait, and northwards along the mid-Patagonian Shelf to the south of the Golfo San Jorge and was characterized by low SST (Fig. 8, Table 4). Group 2 included aggregations located in two areas characterized by high [Chl-*a*]: the Golfo San Jorge and the nearby continental slope (Fig. 8, Table 4). Group 3, contrasting with groups 1 and 2, included almost half of swarms of *M. gregaria*, which were located

in a confined area of the Bahía Grande, north of the eastern entrance of the Straits of Magellan and was distinguished mainly by a high [POC] (Fig. 8, Table 4).

4. Discussion

In this study we show the population expansion of the squat lobster *M. gregaria* through the surveying of its pelagic swarms and we associated their occurrence with habitat characteristics, namely bottom depth, temperature, ocean colour, and particulate organic carbon. Between 2009 and 2014, pelagic swarms increased in occurrence and abundance in both the Beagle Channel and the Argentine Patagonian Shelf. Our data shows that pelagic swarms of *M. gregaria* occurred in
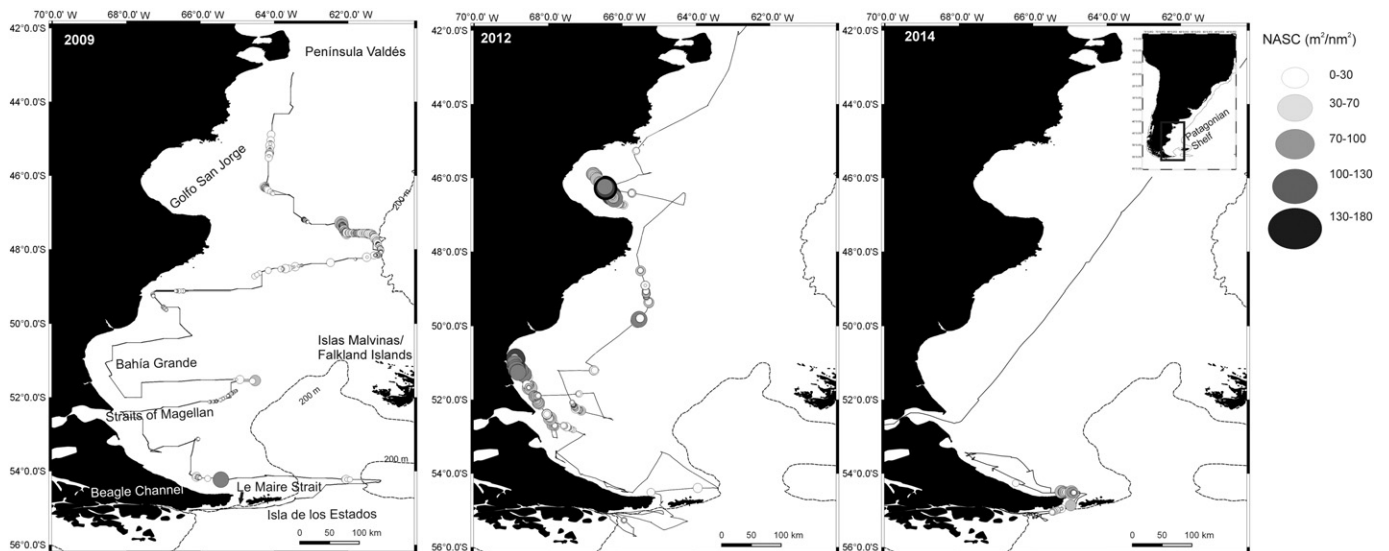

Fig. 3. Horizontal distribution of pelagic swarms of *Munida gregaria* in three years on the Patagonian Shelf. The size of circles is proportional to the NASC (m²/nm²).

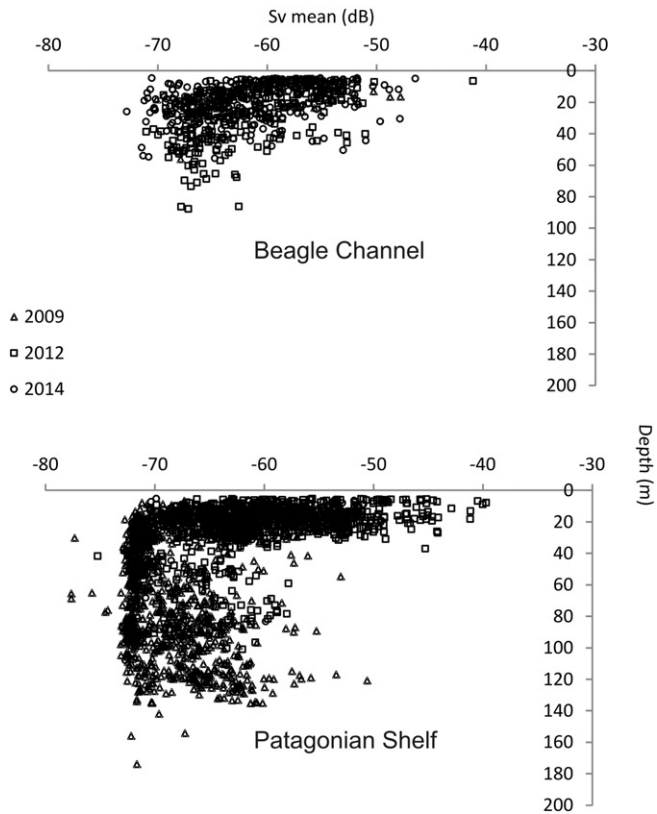**Fig. 4.** Relationship between S_v (dB) mean of the pelagic swarms of *Munida gregaria* and depth in the Beagle Channel (up) and Patagonian Shelf (down).

new locations in 2014 as opposed to 2009, supporting the notion of a population expansion. This work is the first to report the expansion of *M. gregaria* as a process occurring throughout the range of its geographic distribution. So far, historical records of pelagic swarms of this squat lobster have been isolated and anecdotic (e.g. Kawamura, 1976; Matthews, 1932; Rayner, 1935; Tabeta and Kanamaru, 1970). Until 2008, swarms of this species had been not detected in regular acoustic surveys in 1990–2005 in the Patagonian Shelf (Madirolas., pers. obs.) and in 1997–2001 in the Beagle Channel (Tapella, 2002). Since 2009, concurrent records of these pelagic aggregations were observed in different zones of the Patagonian Shelf (Diez et al., 2012; Madirolas et al., 2013; Varisco and Vinuesa, 2010). Simultaneously, an increment of the abundance of the benthic form of *M. gregaria* in certain zones of the Patagonian coasts has been observed (e.g. Golfo San Jorge; Ravalli et al., 2015). Within the Beagle Channel the expansion of swarms was more marked than on the Patagonian Shelf. At the beginning of the present study, in 2009, some areas like Bahía Grande (Fig. 3) did not present acoustic evidence of pelagic swarms of *M. gregaria*. However, in 2012, swarms occurred in this area with high NASC values. By contrast, there were areas, such as the Atlantic Ocean off Tierra del Fuego, in which swarms occurred in very low numbers and density during the studied period. On the Patagonian Shelf, swarms were not present along all of the acoustic transects. In addition, we registered the first record of swarms of *M. gregaria* on the continental shelf-break (ca. 62° W 42° S), which is in contrast with its main sightings reported so far in coastal waters or mid-shelf. This patchy distribution would be related to particular habitat features.

We believe that our comparisons between years and locations are unbiased. On the one hand, occurrence of juvenile *M. gregaria* is highly seasonal in the studied area. Larvae hatches in September every year and metamorphosed juveniles are present after each December. Juveniles can remain in the water column forming swarms during a variable time, typically between 2 and 4 months after metamorphosis (Lovrich,
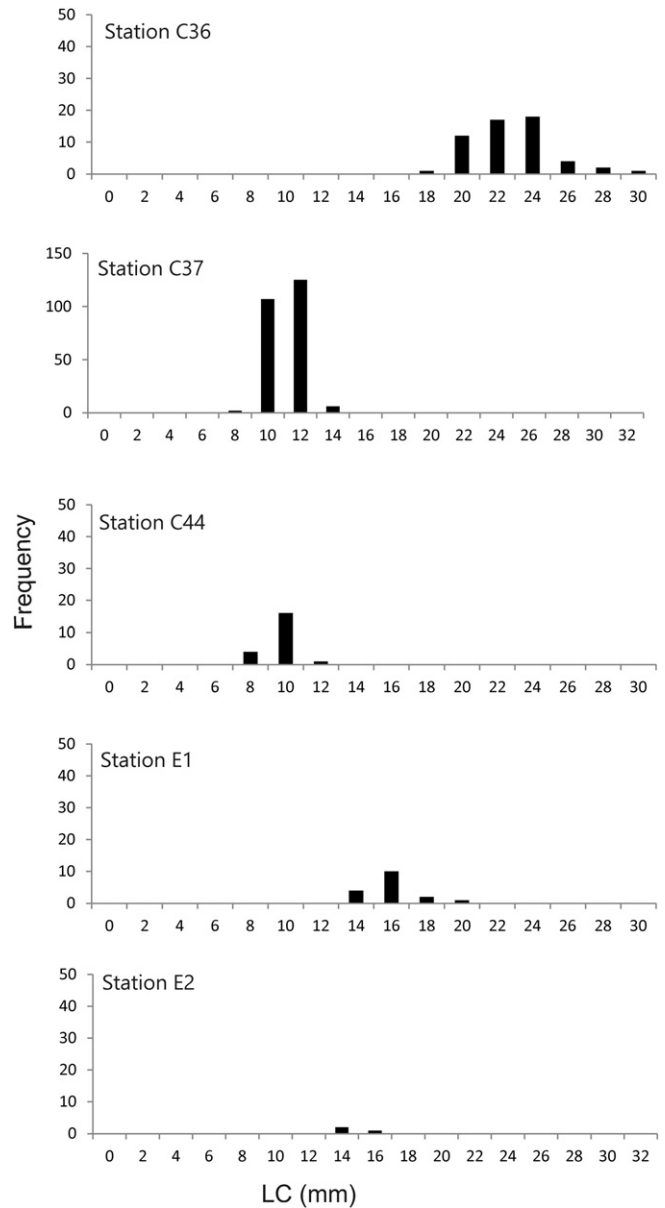

Fig. 5. Size frequency distribution of pelagic *Munida gregaria* during 2012 on the Patagonian Shelf. To a correct visualization of data, selective scales are shown.

1999, Perez-Barros et al., 2007, Vinuesa, 2007, Zeldis, 1985). Therefore, we are confident that our samplings in December and April are comparable because they are surveying the same period of the annual juvenile recruitment. On the other hand, we surveyed two different marine environments: a channel and the open sea. The particularity of the channel, being on average 4 km width, makes swarms to have a higher probability to be detected, because movements in the north-south direction is constrained, and hence the better evidence of expansion from ca. 20% in 2009 to ca. 72% in 2014 in occupancy of surveyed area. Notwithstanding the heterogeneity of tracks, in the continental shelf this pattern of increasing the percent occupancy also increases, sustaining the notion of expansion here presented.

The occurrence of pelagic swarms of Munididae associated to environmental characteristics is well known in the other species with pelagic aggregations. At a regional scale, pelagic aggregations of *P. planipes* off Baja California are linked to zones rich in Chl-*a* at the beginning of spring, when active upwelling takes place (Robinson et al., 2004), and, in turn, determines the pattern of spatial distribution of this species. In addition, acoustic records show that pelagic aggregations of *P. planipes*
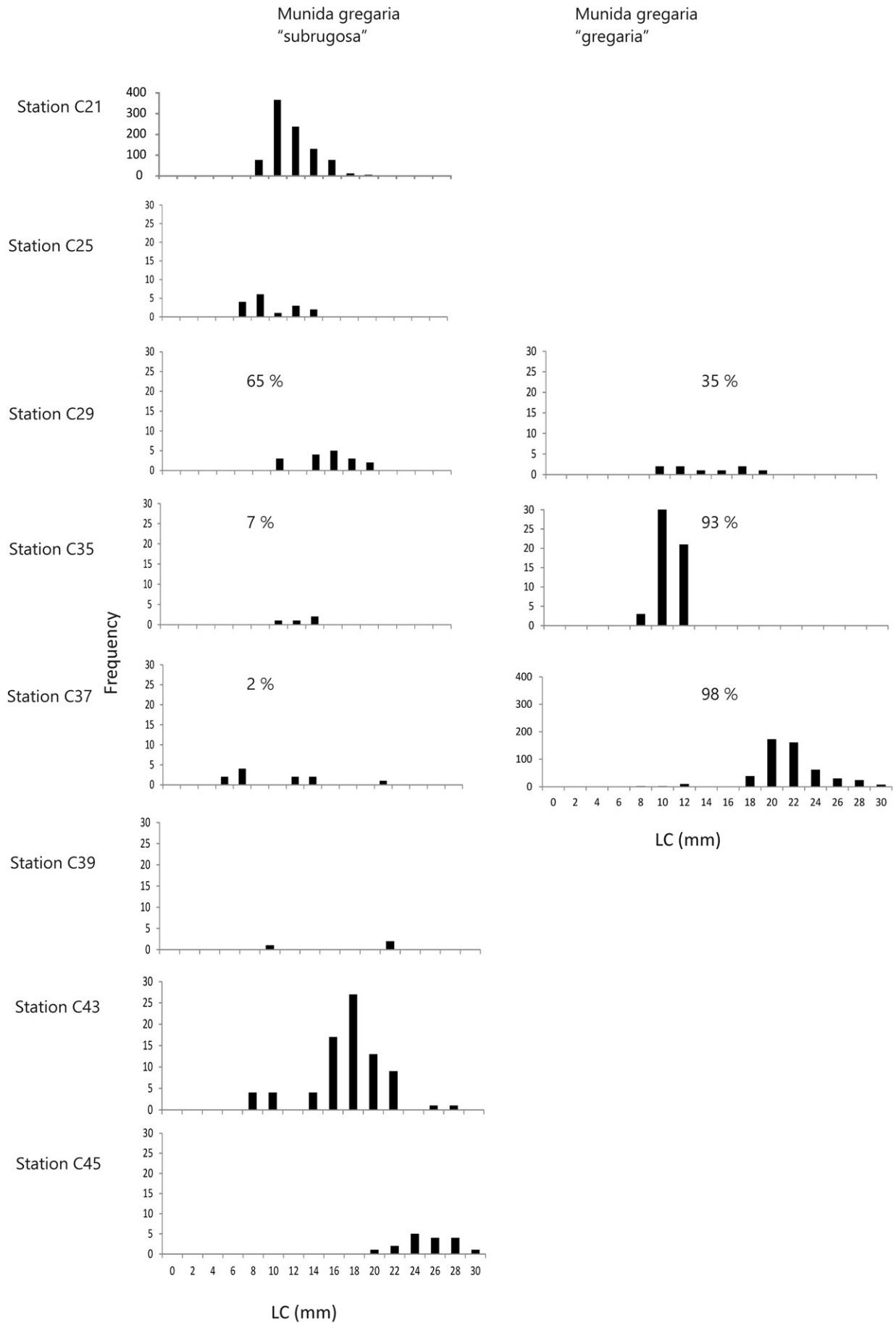
Fig. 6. Size frequency distribution of two morphs of benthic *Munida gregaria* during 2012 on the Patagonian Shelf. Numbers below graphics denote proportion of each morph.

Table 3
Eigenvectors for four variables from the distribution of pelagic swarms of *Munida gregaria* on the Patagonian Shelf, of the first two principal components, which explained 78% of the variation in data set.

Variable	PC1 (46%)	PC2 (32%)
Depth	−0.30	0.73
Sea surface temperature	0.39	0.54
Chl-*a*	0.58	0.31
Particulate organic carbon	0.64	−0.27

perform vertical migrations associated with tides, in which individuals actively swim in the water column during the flood-tide and are close to the bottom during the ebb-tide (Robinson and Gomez-Aguirre, 2004). Off Perú, in one on the most productive upwelling systems of the world, the Humboldt Current, *P. monodon* have also became more abundant than before (Gutiérrez et al., 2008). In this area, swarms of *P. monodon* are restricted to the coldest waters in the upwelling system, spatially constrained to the layer between the sea surface and the oxygen minimum zone (Gutiérrez et al., 2008). Echosoundings show that swarms of *P. monodon* form dense layers above in the oxycline (15–30 m depth) and move vertically during the passage of internal waves (Bertrand et al., 2008). Moreover, in this area *P. monodon* shares and overlaps in its ecological niche with the Peruvian anchovy (Bertrand et al., 2008; Gutiérrez et al., 2008; Gutierrez et al., 2005).

Both in New Zealand and the southern tip of South America, where *M. gregaria* swarms occur, pelagic individuals of this species form dense aggregations that extend horizontally up to several kilometers (Diez et al., 2012; Jillett and Zeldis, 1985; this study), occupying the water column from the sub-surface layer to near the bottom (Diez et al., 2012). At a temporal scale, pelagic swarms of *M. gregaria* can be observed throughout the year in the Beagle Channel and different sites of the Patagonian Shelf (Diez et al., in prep.; Varisco and Vinuesa, 2010). At a spatial scale, swarms are present both at small scale in semi-enclosed bays with small swarms (e.g. Bahía Lapataia, Beagle Channel, Diez et al., in prep.) as well as in open waters like Bahía Grande with swarms of ca. 200 km length. In New Zealand, pelagic swarms of *M. gregaria* are mainly associated with headland fronts: waters with low temperature and salinity, river plume fronts, and internal waves (Jillett and Zeldis, 1985; Zeldis and Jillett, 1982).

We here postulate that expansion of *M. gregaria* occurs through its association with productive areas of the Argentine continental shelf, such as frontal zones. The large area of the Patagonian Shelf studied here, covering 12° of latitude, and 200 km from the coast to the shelf break, show a strong seasonality in primary production (Rivas et al., 2006) and a highly heterogeneous environment (e.g. Acha et al., 2004;

Baldoni et al., 2014; Santoferrara and Alder, 2012; Segura et al., 2013). In this context, positions of major fronts and circulation have a considerable spatial and temporal variation (Acha et al., 2004). Nevertheless this variation, oceanographic fronts control the distribution and intensity of the biological production in the area (Rivas et al., 2006). At small scales of the Patagonian Shelf, frontal zones are associated with an increased vertical mixing which keeps high levels of nutrients in the photic zone even after the spring bloom (Glembocki et al., 2015; Rivas et al., 2006). In the Beagle Channel, differential productive zones are not well known; however, they have presumably a local effect on biological processes. Indeed, in this area swarms of *M. gregaria* generally were observed associated to strong slopes, places in which oceanographic processes at a small scale, like upwellings or resuspension, probably occur.

The three main groups defined by the cluster analysis show that, as it occurs in New Zealand (Jillett and Zeldis, 1985), pelagic swarms of *M. gregaria* on the Patagonian Shelf are probably associated to frontal zones at a regional scale (Fig. 8). Group 1 is located in the coldest waters observed in this study and is related to the cold Patagonian estuarine front that forms a large continuous front on the continental shelf (Acha et al., 2004). This zone is characterized by the combination of waters from the north part of the sub-Antarctic front that are diluted due to an excess of rainfall between the 55–60°S latitudes and the continental discharge originated in the western coast of South America. The flow enters the continental shelf through the Le Maire Strait, receives the contribution of the low salinity and cold water from the Straits of Magellan, and eventually reaches the southern part of the Golfo San Jorge (Acha et al., 2004). Biological information on this zone is very scarce. However, it is known that the fuegian sprat *Sprattus fuegensis*, spawns and recruits in the coastal region off Southern Patagonia associated with this frontal area (Sánchez et al., 1995). *M. gregaria* and *S. fuegensis* overlap spatially and may share their ecological niche (Diez et al., in prep.), comparable to what occurs in coastal waters off Peru, between the squat lobster *P. monodon* and the Peruvian anchovy *Engraulis ringens* (Bertrand et al., 2008). Group 2 is characterized for higher [Chl-*a*] and occurring at the northern shelf and slope, can be separated into two sub-groups with similar habitat characteristics but associated to different frontal zones (Fig. 8): the Argentine shelf-break zone and the Golfo San Jorge. The swarms of *Munida gregaria* recorded in both sub-groups occurred at locations with high [Chl-*a*] (Table 4), which correspond with high productivity frontal areas in both zones (Acha et al., 2004). The environmental features of these zones play a key role to many species, some of them constituting important fisheries in the area such as the Argentine hake *Merluccius hubbsi*, the anchovy *Engraulis anchoita* and the Patagonian scallop *Zygochlamys patagonica*, among others. The area of the Argentine shelf-break where pelagic *M. gregaria* was recorded coincides with the spawning grounds of
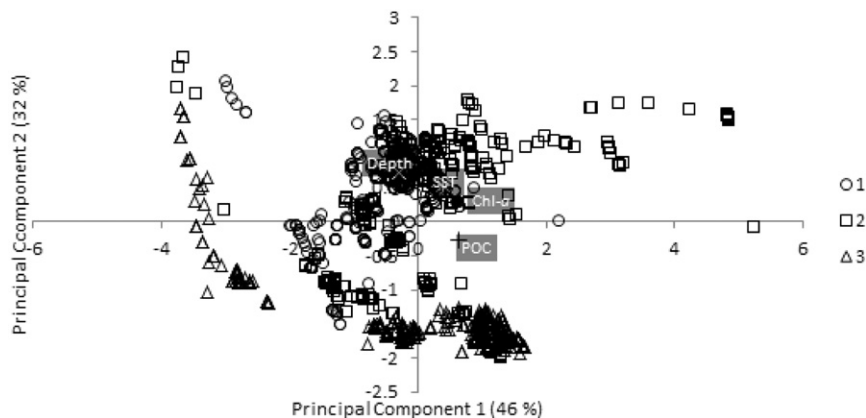

Fig. 7. Principal component analysis for four variables on the distribution of pelagic swarms of *Munida gregaria* on the Patagonian Shelf. Clusters obtained from the cluster K means analysis is shown.

squid *Illex argentinus* (Brunetti and Ivanovic, 1992) and feeding grounds of *M. hubbsi* and *Merluccius australis* (Arkhipkin, 2003). The sub-group observed in the Golfo San Jorge, is related to the Patagonian tidal front, which is a nursery area for the Argentine shrimp *Pleoticus muelleri* and where banks of scallop *Z. patagonica* also occur as a result of the high primary productivity of this area (Acha et al., 2004; Glembocki et al., 2015). Group 3 is associated with Patagonian tidal zone that extends over the Atlantic Patagonian coast from the north of Peninsula

Valdés to Isla de los Estados (Fig. 8). Particularly, the highest proportion of pelagic swarms of *M. gregaria* associated to this zone are related to high [POC] values (Table 4, Fig. 8) and associated to a tidal front located in Bahía Grande (Acha et al., 2004). This front is less known compared to the Peninsula Valdes tidal front, but is similar to several other minor fronts that exist southward (Acha et al., 2004).

The mere evaluation of environmental variables does not explain the expansion of *M. gregaria*. We hypothesize that this expansion may
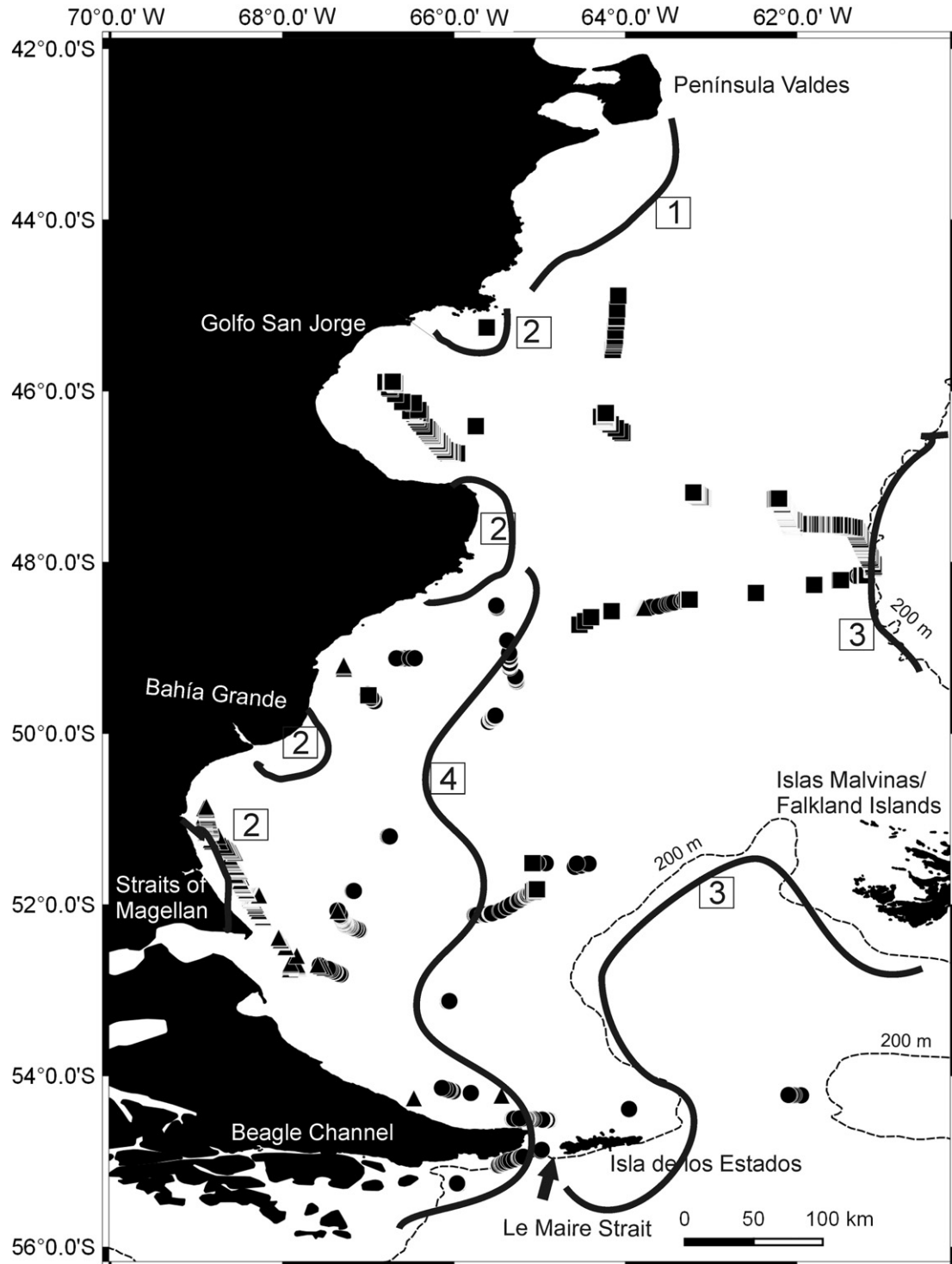

Fig. 8. Distribution of pelagic swarms of *Munida gregaria* in three clusters in relation to frontal zones on the Patagonian Shelf. Circles, squares and triangles denote clusters 1, 2 and 3, respectively. Framed numbers indicate main frontal zones in the area which are shown as black lines. 1: Península Valdés tidal front; 2: Patagonian tidal fronts; 3: Argentine shelf-break front; 4: cold Patagonian estuarine front (Acha et al., 2004).

be the result of the combination of advantageous environmental conditions and biological factors. Intrinsic features of the early life history of *M. gregaria* probably allow them to adapt and exploit productive areas of the Patagonian continental shelf. *M. gregaria* has phenotypic plasticity, with two morphs of postmetamorphic individuals with different habits: "gregaria" pelagic/benthic and "subrugosa" exclusively benthic (Pérez-Barros et al., 2008). *M. gregaria* has an extended planktotrophic larval development with five or six zoea stages and one megalopa stage (Lovrich, 1999; Perez-Barros et al., 2007). The existence of two morphs of megalopae suggests that the zoea V is the ontogenetic phase at which one of the two morphs will develop (Bacardit, 1986; Rayner, 1935; Varisco, 2012). In some species, it is known that their feeding performance and diet composition during larval phases can induce the development into different morphotypes or sex reversal (Parsons and Robinson, 2007; Zupo, 2000). Because metamorphosis requires a high energy expenditure (Anger, 2001), changes in food composition (e.g. phytoplankton; Fricke et al., 2015) will likely affect the metamorphosis in an adaptive way, that results advantageous for its development into one or another morph. Food quality positively affects the recruitment success in other invertebrate species (Parsons and Robinson, 2007; Toupoint et al., 2012) and hence changes in phytoplankton composition on the continental shelf (Segura et al., 2013) is here postulated as inducing the metamorphosis of *M. gregaria* into its pelagic form. This will be also favoured by the existence of high productive areas as marine fronts that allow the survival of the pelagic individuals, a niche that can be exploited by such a plastic species. Moreover, high population densities of the benthic individuals as occurred previously and during our study (Ravalli et al., 2012, 2015) may promote the formation of pelagic swarms. In such dense benthic aggregations, squat lobsters face a great risk of negative intraspecific interactions like cannibalism, which controls population numbers (Thiel and Lovrich, 2011; Zeldis, 1985). Hence, low density of benthic individuals allows new settlers to remain at the bottom indefinitely. By contrast, if benthic density is high, potential settlers will extend the swarming period and reach sexual maturity in the water column. Pelagic swarms periodically move to the bottom probably to feed (Zeldis, 1985), which is supported by the presence of sediment, particulate organic matter and benthic macroalgae in their stomach content (Diez et al., 2012). Therefore, swarming could be a strategy to avoid cannibalism, as reported for the other two species of squat lobsters that can shoal, *P. planipes* and *P. monodon* (Gómez-Gutiérrez and Sanchez-Ortiz, 1997; Zeldis, 1985). Environmental factors such as phytoplanktonic food resources that promote metamorphosis into the gregaria form and cannibalism avoidance could be acting together to result in a population enhancement, successfully colonizing new environments or areas of the continental shelf, such as found in this study by echosounding.

The recent increase in occurrence of pelagic swarms of *M. gregaria* has been observed at many different locations simultaneously [e.g. Golfo San Jorge, Beagle Channel, Golfo Nuevo, Golfo San Matías (ca. 42°S 65°W); Diez et al., 2012; Madirolas et al., 2013; Varisco and Vinuesa, 2010]. These areas exhibit different oceanographic and biological features, and fishing pressure. The reported phenotypic plasticity of *M. gregaria* (Pérez-Barros et al., 2011, 2008) could allow to exploit different resources, either benthic or neritic, or to survive under new environmental conditions. Although it is known that *M. gregaria* is an abundant species on the Patagonian Shelf (Spivak, 1997), it is of interest to know why this species is occupying new areas and whether migration is possible. Supported by results of the Beagle Channel, we postulate that migration patterns are not present on the Argentine Patagonian Shelf. The Beagle Channel is a semi-enclosed environment and its geomorphological characteristics, i.e. shallow waters in its eastern entrance towards the Atlantic Ocean, allow a limited exchange of pelagic species with the open ocean (Antezana, 1999; Isla et al., 1999). Hence, the increased number of pelagic swarms of *M. gregaria* in the Beagle Channel is likely evidence of population expansion rather than indication of immigration movements.

Table 4
Mean values (standard deviation) of environmental variables for individual clusters from a cluster K means analysis (Cluster) and from all acoustic records (Survey) of pelagic swarms of *Munida gregaria* in different years in the Patagonian Shelf. SST is surface seawater temperature; Chl-*a*: chlorophyll a; POC: particulate organic carbon.

Cluster	Depth (m)	SST (°C)	Chl-*a* (mg/m^3)	POC (mg/m^3)
1	120.81 (49.80)	8.94 (1.34)	0.93 (0.44)	155.50 (46.09)
2	129.95 (26.85)	11.59 (1.29)	2.46 (1.39)	216.68 (44.11)
3	44.37 (12.25)	9.27 (0.66)	1.71 (0.48)	283.37 (54.74)
Survey				
December 2009	132.59 (32.84)	10.64 (1.22)	2.52 (1.44)	211.32 (50.52)
April 2012	78.25 (44.52)	10.34 (1.87)	1.44 (0.50)	238.46 (64.41)
April 2014	130.87 (50.86)	7.16 (0.36)	0.38 (0.07)	80.84 (13.63)

In addition to the aforementioned hypothesis of changes in food quality, some other changes in the ecosystem could be also contributing to an increase in the rate of larval dispersal, such as an increase of larval survival and a higher recruitment rate, among other life history features. Larval stages, juveniles and adult *M. gregaria* are prey items to a wide spectrum of predators, such as marine mammals (e.g. Koen Alonso et al., 2000), seabirds (e.g. Scioscia et al., 2014) other crustaceans (Balzi, 2006; Comoglio and Amin, 1996), and squids (Brunetti et al., 1999). Among fishes, *M. gregaria* is prey of about 30 different species (Bellegia, 2014; Rodriguez and Bahamonde, 1986; García de la Rosa and Sánchez, 1997; Sanchez and Prensky, 1996), some of which have been target species of the commercial fishery for decades. A decline in predator pressure by any of these species could also contribute to the expansion and occurrence of squat lobster swarms in new areas of the Patagonian Shelf.

Acknowledgments

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